

MERMITHID (NEMATODA) PARASITES OF SPIDERS AND HARVESTMEN

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ABSTRACT

Nematode parasites of spiders and harvestmen are restricted to members of the family Mermithidae. A literature review shows that nematode parasitism of arachnids is worldwide and at least 51 species of spiders and harvestmen have been recorded as hosts of mermithid nematodes. Infected spiders have varied habits and it is postulated that two types of parasite life cycles probably exist and that the indirect life cycle (involving a paratenic host which falls prey to the arachnid) is probably the common type.

INTRODUCTION

Representatives of the family Mermithidae are the only nematodes known to parasitize spiders. Their effect on spiders is similar to that on other arthropod hosts, namely host mortality at the time of parasite emergence.

The difficulty in rearing adult mermithids from postparasitic juveniles that have emerged from parasitized spiders has prevented a systematic assessment of spider mermithids. However, it is apparent that mermithid parasitism of spiders is widespread and occurs in various habitats. The present work tabulates previous instances of these associations, adds some, and discusses the host parasite relationship. Reports of spider parasitism by horsehair worms are not discussed here. The latter, commonly referred to as *Gordius*, are not nematodes and belong to a separate phylum, the Nematomorpha. Early reports of spiders parasitized by the horsehair worms may actually have involved mermithid nematodes and vice versa. The adult forms of both groups are similar superficially and may have the same type of life cycle.

RESULTS AND DISCUSSION

Parasite identification.—Records of spider parasitism by mermithid nematodes are summarized in Table 1. E. Schlinger gave me mermithids that emerged from spiders in New Guinea and New Zealand but they have not been included in the Table since the hosts were not identified. Such is the case for a parasitized male clubionid from Papua, New Guinea, that L. N. Sorkin had in his collection.

Table 1.—Records of mermithid nematode parasitism in spiders and harvestmen.

| Host | Parasite identified as | Reference |
|--|---|---------------------------------------|
| <i>Argyoneta aquatica</i> (Clerck) | <i>Mermis albicans</i> von Siebold | Menge, 1866 |
| <i>Atypoides riversi</i> O. P.-Cambridge | unknown | Vincent, in press |
| <i>Cesonia bilineata</i> (Hentz) | <i>Aranimeris aptispicula</i> Poinar and Benton | Poinar and Benton, in press |
| <i>Coelotes inermis</i> (L. Koch) | unknown | Müller, 1983 |
| <i>Combridgea</i> sp. [New Zealand] | unknown | Lowe (pers. comm.) |
| <i>Diaea dorsata</i> Fabricius | <i>Arachnomermis dialaensis</i> Rubtsov | Rubtsov, 1980 |
| <i>Drassodes</i> sp. [Canada] | unknown | Holmberg (pers. comm.) |
| <i>Lycosa riparia sphagnicola</i> Dahl. | <i>Mermis</i> sp. | Holm, 1941 |
| <i>Lycosa</i> sp. [Argentina] | unknown | Doucet (pers. comm.) |
| <i>Drassus lucifugus</i> (Walckenaer) | unknown | von Siebold, 1843 |
| <i>Epeira diadema</i> Clerck | unknown | Walckenaer, 1883 |
| <i>Geolycosa patellonigra</i> Wallace [U.S.A.] | unknown | Miller (pers. comm.) |
| <i>Gnaphosa</i> sp. [U.S.A.] | unknown | Sorkin (pers. comm.) |
| <i>Homolophus biceps</i> (Thorell) [Canada] | unknown | Holmberg (pers. comm.) |
| <i>Lycosa saccata</i> Latreille | <i>Mermis</i> sp. | Holm, 1941 |
| <i>Lycosa scutulata</i> Hentz | <i>Filaria lycosae</i> Haldeman | Haldeman, 1847, 1851 |
| <i>Lycosa</i> sp. | <i>Mermis</i> sp. | Bristowe, 1941 |
| <i>Lycosa</i> sp. | <i>Filaria</i> | Kryger, 1910 |
| <i>Lycosa</i> sp. | <i>Mermis robusta</i> Leidy | Leidy, 1856 |
| <i>Lycosa tarsalis</i> Thorell | <i>Mermis</i> sp. | Holm, 1941 |
| <i>Lycosa verisimilis</i> Montgomery | <i>Mermis</i> sp. | Montgomery, 1903 |
| <i>Lycosa vorax</i> Walckenaer | unknown | von Siebold, 1854 |
| <i>Micryphantès bicuspidatus</i> C. L. Koch | unknown | von Siebold, 1848 |
| <i>Miranda ceropegia</i> C. L. Koch | unknown | Hoppe, 1796 |
| <i>Misumenops</i> sp. | <i>Aranimeris aptispicula</i> Poinar and Benton | Poinar and Benton, in press |
| <i>Mitopus morio</i> (Fabricius) | <i>Agameris incerta</i> (Steiner) | Stipperger, 1928 |
| <i>Opilio</i> sp. | <i>Hexameris</i> sp. | Unzicker and Rotramel, 1970 |
| <i>Opilio</i> sp. | <i>Mermis</i> sp. | Kästner, 1928 |
| <i>Paecilaemana quadripunctata</i> Goodnight & Goodnight | unknown | Goodnight and Goodnight (pers. comm.) |

Table 1.—Continued

| Host | Parasite identified as | Reference |
|--|---|-----------------------------|
| <i>Pardosa glacialis</i> (Thorell) | <i>Hexameris</i> sp. | Leech, 1966 |
| <i>Pardosa hortensis</i> (Thorell) | unknown | Parker and Roberts, 1974 |
| <i>Pardosa lugubris</i> (Walckenaer) | <i>Amphimermis</i> (?) <i>pardosensis</i> Rubtsov | Rubtsov, 1977 |
| <i>Pardosa nigropalpis</i> Emerton | <i>Mermis</i> sp. | Montgomery, 1903 |
| <i>Pardosa riparia</i> (C. L. Koch) | <i>Amphimermis pardosensis</i> Rubtsov | Rubtsov, 1977 |
| <i>Pardosa scita</i> Montgomery | <i>Mermis</i> sp. | Montgomery, 1903 |
| <i>Pardosa</i> sp. | <i>Agameremis decaudata</i> C. S. C. | Kaston, 1945 |
| <i>Pardosa</i> sp. | <i>Arachnomermis araneosa</i> Rubtsov | Rubtsov, 1978 |
| <i>Pardosa vancouveri</i> Emerton [Canada] | unknown | Holmberg (pers. comm.) |
| <i>Peucetia viridans</i> (Hentz) [U.S.A.] | unknown | Landau (pers. comm.) |
| <i>Phalangium cornutum</i> Linn. | <i>Filaria phalangii</i> Haldeman | Haldeman, 1851 |
| <i>Phalangium opilio</i> Linn. | unknown | Pfeifer, 1956 |
| <i>Phalangium opilio</i> Linn. | <i>Filaria truncatula</i> Rudolphi | Rudolphi, 1819 |
| <i>Phidippus borealis</i> Banks [U.S.A.] | unknown | Cutler (pers. comm.) |
| <i>Phidippus clarus</i> Keyserling | <i>Agameremis decaudata</i> C. S. & C. | Kaston, 1945 |
| <i>Phidippus putnamii</i> (Peckham & Peckham) [U.S.A.] | unknown | Cutler (pers. comm.) |
| <i>Phidippus</i> sp. | <i>Aranimeris aptispicula</i> Poinar & Benton | Poinar and Benton, in press |
| <i>Pseudicus</i> sp. [U.S.A.] | unknown | Sorkin (pers. comm.) |
| <i>Salticus formicarius</i> Latreille | unknown | Bertkau, 1888 |
| <i>Schizocosa saltatrix</i> (Hentz) | <i>Mermis</i> sp. | Montgomery, 1903 |
| <i>Schizocosa</i> sp. [U.S.A.] | unknown | Sorkin (pers. comm.) |
| <i>Sosippus floridanus</i> Simon | unknown | Kaston, 1945 |
| <i>Tarentula inquilina</i> Thorell | <i>Mermis</i> sp. | Bertkau, 1888 |
| <i>Tetragnatha</i> sp. [Canada] | unknown | Sorkin (pers. comm.) |
| <i>Tetragnatha</i> sp. | unknown | Sorkin (pers. comm.) |
| <i>Theridion ovatum</i> (Clerck) | <i>Mermis</i> sp. | Bristowe, 1931 |
| <i>Tibellus oblongus</i> (Walckenaer) | unknown | Holmberg (pers. comm.) |
| <i>Tmarus</i> sp. | <i>Aranimeris aptispicula</i> Poinar & Benton | Poinar and Benton, in press |
| <i>Verrucosa arenata</i> (Walckenaer) | <i>Aranimeris aptispicula</i> Poinar & Benton | Poinar and Benton, in press |
| <i>Wadotes</i> sp. | <i>Aranimeris aptispicula</i> Poinar & Benton | Poinar and Benton, in press |
| <i>Wulfilia alba</i> (Hentz) | <i>Aranimeris aptispicula</i> Poinar & Benton | Poinar and Benton, in press |
| <i>Xysticus deichmanni</i> Soerensen | <i>Aranimeris aptispicula</i> Poinar & Benton | Poinar and Benton, in press |
| <i>Xysticus funestus</i> Keyserling | <i>Hexameris</i> sp. | Leech, 1966 |
| <i>Zora maculata</i> O. P.-Cambridge | <i>Hexameris</i> sp. | Kaston, 1945 |
| | <i>Filaria</i> sp. | Kryger, 1910 |

The earliest reported incidence of mermithid parasitism of spiders was by Hoppe in 1796. No attempt was made to describe the parasite. In 1833, Walckenaer cited a *Filaria* from *Aranea diadema*. At that time, the name *Filaria* was used as a collective genus name for representatives of various groups, especially the larger parasitic worms, such as representatives of the Mermithidae. It had no taxonomic significance. Kryger (1910) also cited *Filaria* from *Lycosa* sp. and *Zora maculata*. In 1819, Rudolphi described mermithids he obtained from *Phalangium cornutum* and *P. opilio* as *Filaria truncatula*. However, his description was very brief and based on general characters found in the postparasitic juveniles. Since adult characters are needed for proper taxonomic placement, this must be cited as a species inquirenda. Also included in this category are *Filaria phalangii* Halde- man 1851 and *Filaria lycosae* Haldeman 1847.

Later, the genus *Mermis* was used in a broad sense to represent members of the family Mermithidae. It and the frequently used binomial, *Mermis albicans*, were assigned to a range of species collected from arthropods. However, as in the case of *Filaria*, these names were used in a collective sense and either lacked a description or the description was so general that it was useful only to family level. Thus the citations listed in Table 1 for Menge (1866), Holm (1941), Bristowe (1931; 1941), Montgomery (1903), Kästner (1928) and Bertkau (1888) when *Mermis* sp. or *Mermis albicans* is mentioned must stand as species inquirendae. Kaston (1945) cited *Agamermis decaudata* as a parasite of *Pardosa* sp. and *Phidippus clarus*. Those nematodes were identified by G. Thorne, basically a plant nematologist. Since he was probably examining juveniles, it is doubtful that a specific designation could have been possible. Also, *A. decaudata* is a parasite of Orthoptera and has not otherwise been reported from spiders. It is my contention that this was a misidentification.

Reports of a *Hexameris* sp. parasitizing *Xysticus deichmanni*, *X. funestus* and *Pardosa glacialis* (Kaston, 1945) (Leech, 1966) are also not exact since postparasitic juveniles were examined and only rarely can a genus be determined from these stages. More recently, Rubtsov described *Amphimermis pardosensis* from *Pardosa riparia* (1977), *Arachnomermis araneosa* from *Pardosa* sp. (1978) and *Arachnomermis dialaensis* from *Diaea dorsata* (1980). The descriptions of these species are based on postparasitic juveniles and again, their true identity remains unknown. From what we now know about mermithid morphology and systematics, all of the above mentioned mermithids from spiders have no systematic position in the classification of the Mermithidae and might well be placed in the collective genus, *Agamermis*, erected to receive mermithids that could not be placed in existing genera (Poinar and Welch, 1981).

The only completely described mermithid parasite of spiders is *Aranimeris aptispicula* Poinar and Benton (in press). The description is based on adult characters comparable with those of existing genera.

Effects of parasitism.—External symptoms of mermithid parasitism of spiders usually are associated with the size and shape of the host's body. A swollen abdomen is a common symptom and Leech (1966) noted that parasitized *P. glacialis* had a lopsided or greatly enlarged opisthosoma, an altered epigynum, malformed palpi, legs that were shorter and thicker than normal and poorly developed or absent male secondary sexual characteristics. It is possible to see the coils of the parasite through the host's integument since the mermithid usually occupies the entire abdomen and occasionally the cephalo- thorax. Parasitic castration was noted by Bertkau (1888) in a *Tarentula inquilina* attacked by a mermithid.

Infection signs generally start with a reduction or absence of the digestive gland. In extreme examples, other organs may also be reduced. Leech (1966) commented that

parasitism of *P. glacialis* resulted in the loss of the main prosomatic muscles, the entire digestive system and the entire reproductive system.

Behavioral changes in parasitized spiders have also been noted. Leech (1966) (and personal correspondence) mentioned that some infected individuals of *P. glacialis* were sluggish and did not attempt to escape when approached. During the week before the

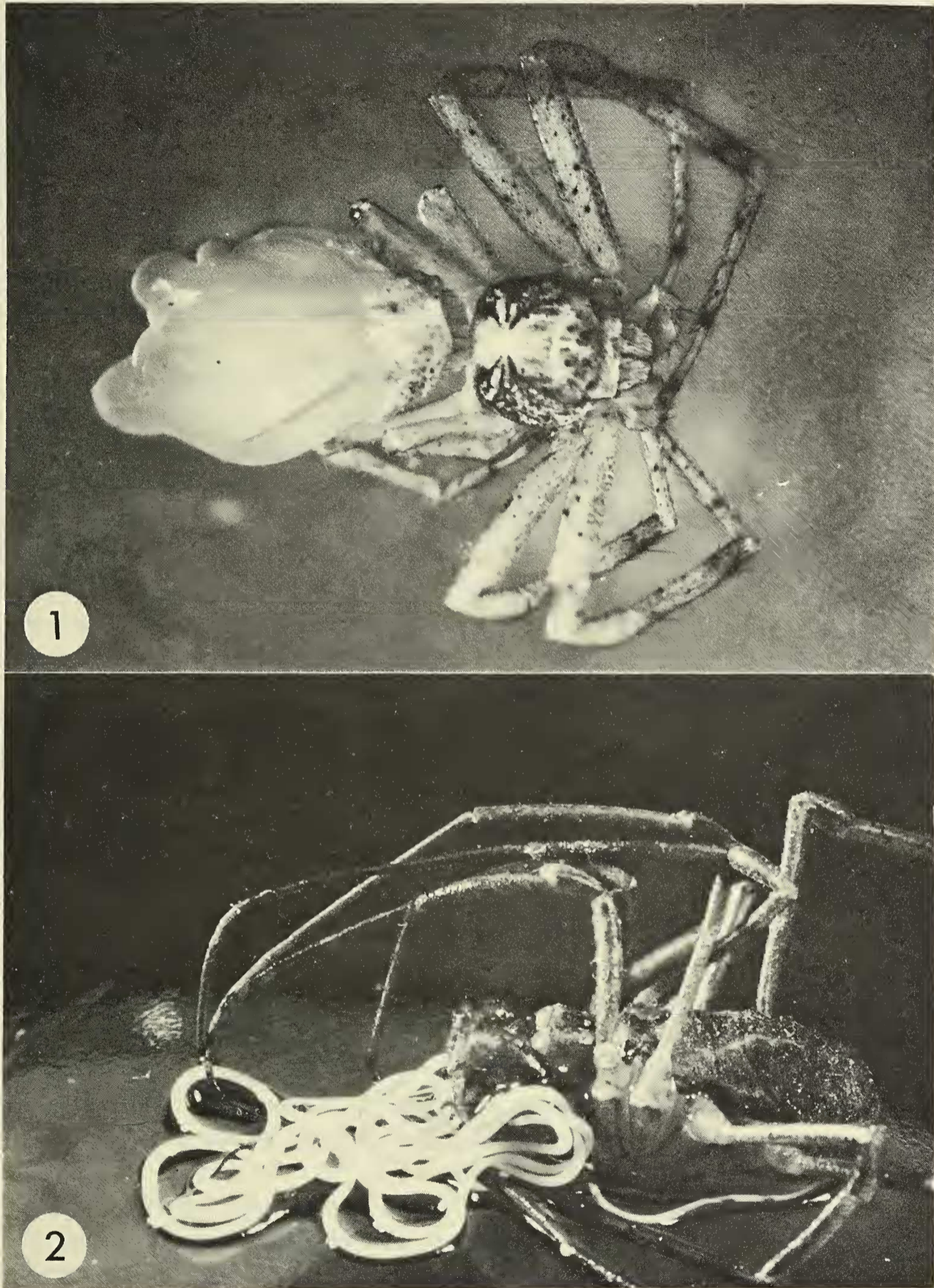


Fig. 1.—Coils of *Aranimeris aptispicula* Poinar and Benton filling the abdominal cavity of the spider, *Tmarus* [probably *angulatus* (Hentz)]. (Photo by the author; specimen from C. Benton). (Mag. x 10).

Fig. 2.—A postparasitic juvenile mermithid that has just emerged from its phalangid host, a male *Protolophus* sp. (Photo by Pat Craig). (Mag. x 5).

parasites emerged the spiders ceased feeding but drank a lot of water. This attractiveness to water was noted in infested *A. aptispicula* which would come out of neighboring woods and fields to find a source of water.

Kaston (1945) presented some evidence that mermithids retard the development of their spider hosts.

Incidence of infection.—Most of the reports of mermithid parasitism of spiders mention only a single incidence of infection. Leech (1966) noted that 1% of the *Pardosa glacialis* he collected were parasitized and that most were females. He mentioned that the rate might have been higher since the infection is very hard to detect in young spiders.

Color of parasites.—Certain species of mermithids can be recognized by their color and both Haldeman (1851) and Leidy (1856) mentioned that upon emergence, the nematodes were pale pink to reddish. The former author noted that the color changed to yellowish after the specimen was heat-killed. This color change was also noted by Poinar and Benton (in press) in *A. aptispicula*. Emerging individuals were pinkish, yellowish and occasionally green, but all became white after some days in water. The initial color may have been acquired from the host.

Life cycle of mermithids attacking spiders.—Although the life history of no spider mermithid is completely known, *Aranimeris aptispicula* is one that probably possesses an indirect life cycle. Its occurrence in a wide range of spiders suggests this. In this type of development, the females deposit eggs in an aquatic habitat. The eggs are ingested by immature insects and the infective stage mermithid hatches, penetrates the gut wall, invades the parenteral tissues of the host and then enters dormancy. Thus when the host matures, it carries the parasite. When one of these paratenic hosts falls prey to a spider and is eaten, the nematode becomes active, enters the spider's hemocoel and resumes development. Such a life cycle has been shown to occur in *Pheromermis pachysoma*, a parasite of yellowjackets (Poinar et al. 1976).

However, from the descriptions of some postparasitic juvenile mermithids that emerged from spiders, it is obvious that at least one other mermithid species attacks spiders in North America. This species could well have a direct cycle, that is, one where the infective stage emerging from the egg enters a young spider by direct penetration through the integument and initiates development. A second host is not involved in such a cycle.

Type of spiders attacked.—Spiders that are attacked by mermithids demonstrate a wide range of behavior and habitat preference. Thus, it is not just ground-stratum hunters that show mermithid parasitism but also orb web weavers, aquatic forms, plant climbers, and even crab spiders that catch insects attracted to flowers. Food preference for parasitized spiders is not restricted to any particular group of insects. It is interesting to note that all spiders found parasitized would have an opportunity to feed on adult insects which possess an aquatic larval stage (e.g. Chironomidae, Culicidae, Trichoptera). Such insects would make ideal paratenic hosts.

Recommended handling of mermithids.—Upon noticing the emergence of a mermithid from a spider host, the investigator should place the parasite in a small amount of water in a glass container with a layer of sand in the bottom. It should be left until it has molted (a single molt composed of the final two shed cuticles) to the adult stage which normally occurs within a month. During this time, the water should be changed daily to avoid the accumulation of fungi which can kill the parasite. Adult stages can be recognized by the appearance of the vulva in the female and the spicules (copulatory organs) in the male [see Poinar (1983) for figures of the appearance and location of these structures].

The adults should be killed by placing them in water heated to 50-60°C. After death, they can be fixed in 3% formalin or 70% alcohol for taxonomic studies. If the living worms are placed directly into fixative when they emerge from the spiders, further taxonomic studies will be prevented.

ACKNOWLEDGMENTS

The author would like to express his sincere appreciation and gratitude to Pat Craig for his assistance in the preparation of this manuscript. Thanks are also extended to the following individuals for submitting material cited in the text; R. G. Holmberg, L. Vincent, M. Doucet, G. Landau, C. L. B. Benton, Jr., E. L. Schlinger, B. Cutler, G. L. Miller, J. C. Cokendolpher, G. Lowe and L. N. Sorkin.

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Manuscript received May 1984, revised August 1984.